

Slow and steady wins the race? Future climate and land use change leaves the imperiled Blanding's turtle (*Emydoidea blandingii*) behind

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ABSTRACT

Climate change is accompanied by shifts in species distributions, as portions of current ranges become less suitable. Maintaining or improving landscape connectivity to facilitate species movements is a primary approach to mitigate the effects of climate change on biodiversity. However, it is not clear how ongoing changes in land use and climate may affect the existing connectivity of landscapes. We evaluated shifts in habitat suitability and connectivity for the imperiled Blanding's turtle (*Emydoidea blandingii*) in Wisconsin using species distribution modeling in combination with different future scenarios of both land use change and climate change for the 2050s. We found that climate change had significant effects on both habitat suitability and connectivity, however, there was little difference in the magnitude of effects among different economic scenarios. Under both our low- and high-CO₂ emissions scenarios, suitable habitat for the Blanding's turtle shifted northward. In the high-emissions scenario, almost no suitable habitat remained for Blanding's turtle in Wisconsin by the 2050s and there was up to a 100,000-fold increase in landscape resistance to turtle movement, suggesting the landscape essentially becomes impassable. Habitat loss and landscape resistance were exponentially greater in southern versus northern Wisconsin, indicating a strong trailing edge effect. Thus, populations at the southern edge of the range are likely to “fall behind” shifts in suitable habitat faster than northern populations. Given its limited dispersal capability, loss of suitable habitat may occur at a rate far faster than the Blanding's turtle can adjust to changing conditions via shifts in range.

1. Introduction

In response to climate change, many species may need to move large distances and colonize new areas when climate conditions within their current range become unsuitable (Chen et al., 2011). However, land use change and landscape fragmentation may limit opportunities for species to reach newly suitable areas (Hamilton et al., 2015). Landscapes can be viewed as a mosaic of habitat and non-habitat patches and, in human-dominated landscapes, many of the non-habitat patches result from human use (Franklin and Lindenmayer, 2009; Lindenmayer et al., 2008). Protected areas are a key conservation tool to maintain

biodiversity (Joppa et al., 2008; Rodrigues et al., 2004), although it is not clear how future changes in land use and climate will influence their effectiveness (Fleishman et al., 2011). A commonly proposed strategy for conserving species is to establish habitat corridors and patches that can function as stepping stones to improve connectivity among protected areas (Heller and Zavaleta, 2009; Krosby et al., 2010). The assumption is that a network of connected protected areas will reduce impediments to species dispersal and thereby facilitate movement among resource patches (Griffith et al., 2009; Beier and Brost, 2010). With limited funding available for conservation, it is critical that such investments account for both current and future threats to

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maximize and sustain gains (Mairota et al., 2013; Merenlender et al., 2009).

The majority of the land area of the planet is either used by humans or altered by them (Foley et al., 2005; Sanderson et al., 2002; Vitousek and Mooney, 1997). Land cover outside of protected areas includes a range of cover types, from urban to row crops to areas that include some natural or semi-natural elements. The type of land cover strongly affects potential movement of species through the landscape (Baum et al., 2014; Hamilton et al., 2013). The distribution and arrangement of both natural elements and anthropogenic land use within a landscape matrix affects its ecological function and, therefore, the condition of the matrix must be considered in any planning for habitat connectivity (Franklin and Lindenmayer, 2009; Lindenmayer et al., 2008; Mairota et al., 2013).

To address the consequences of human-induced global change, adaptation strategies such as adjustments to socio-economic and land use practices are often proposed in an adaptive management framework, i.e. the process of adjusting management practices to maximize benefit as we learn about a system (Smith et al., 2000b). Improving habitat connectivity is one of the primary adaptation strategies in this context used for enhancing resilience (i.e., the ability of a system to recover from perturbations) within biological systems (Griffith et al., 2009; Mori et al., 2013). Connectivity reflects the degree to which a landscape facilitates or impedes movements among habitat patches (Taylor et al., 1993), and is an important component of the resilience of ecological systems because high connectivity facilitates species movements among patches (DeFries et al., 2007; Hansen and DeFries, 2007). Connectivity is affected by both habitat loss (i.e., overall reduction in the amount and quality of habitat) and habitat fragmentation (i.e., the breaking apart of habitat). Habitat loss has consistent negative impacts to biodiversity, while habitat fragmentation effects are weaker and more variable (Fahrig, 2003). Connectivity depends on the spatial patterns of habitat, which are affected by land use, and therefore adjustments to land use are the primary method for improving connectivity.

Corridors and stepping stones are, by definition, embedded in a matrix of variably hospitable land cover (Baum et al., 2014; Beier and Noss, 1998). Habitat corridors are linear habitat patches connecting two or more larger blocks of habitat (Beier and Noss, 1998). Stepping stones, on the other hand, are a series of small habitat patches that connect otherwise isolated habitat blocks (Baum et al., 2014). While there has been debate about the effectiveness of corridors, both literature reviews and empirical studies have demonstrated their conservation value (Damschen et al., 2006; Noss, 1987; Simberloff et al., 1992; Beier and Noss, 1998; Gilbert-Norton et al., 2010; Haddad et al., 2003; Haddad and Tewksbury, 2005). Stepping stones tend to have weaker effects but are still useful in many situations (Baum et al., 2014; Leidner and Haddad, 2011), and in some cases may be critical for improving landscape connectivity (Krosby et al., 2010; Saura et al., 2013).

Range shifts driven by climate change have already been documented for a number of species and in the future large changes in species distribution and community composition are anticipated (Chen et al., 2011; Heller and Zavaleta, 2009; Thuiller, 2004), and one of the primary ways to meet the conservation goal is by maintaining and, where needed, improving connectivity. For connectivity assessments to be most valuable for conservation decisions, it is crucial to examine both current functional connectivity - i.e., the amount and spatial arrangement of habitat that a given species uses to move among areas that are permanently occupied - (Crooks and Sanjayan, 2006; Tischendorf and Fahrig, 2000a, 2000b) and likely future changes, potential threats to, and shifts in, connectivity (Mori et al., 2013; Smith et al., 2000a). Incorporating threat into conservation decisions is crucial to maximizing outcomes from the investment of limited funding (Merenlender et al., 2009). Identification of future threats is recognized as a priority by the U.S. Fish and Wildlife Service National Wildlife Refuge System (Griffith et al., 2009) and understanding the potential

future effects of matrix land use and climate change on protected areas is essential for guiding conservation policy (Fleishman et al., 2011). Assessing the effects of future change on connectivity among protected areas should thus be an important aspect of conservation planning, yet this has rarely been done (Piquer-Rodríguez et al., 2012; Rouget et al., 2003). However, quantifying future connectivity is critical given its reliance on spatial arrangement of habitat patches, (Fahrig, 2003; Goodwin and Fahrig, 2002). Projections of future conditions can be relatively accurate at estimating proportional change across broad areas, but spatially explicit estimates are far more challenging, owing to the difficulty of identifying which specific parcels of land are likely to undergo changes (Radeloff et al., 2012). In general though, when projecting future conditions, the combination of exploring potential scenarios and constructing predictive models is useful for increasing the value of ecological research for management application (Coreau et al., 2009). The comparison of future scenarios can provide important insights about biodiversity and other ecological resources (Gude et al., 2007; White et al., 1997).

Our goal here was to evaluate current and future potential functional connectivity among protected areas in Wisconsin, U.S., for the Blanding's turtle. We chose Blanding's turtle because it is a widely distributed and declining species that faces similar threats to landscape movement across its entire range. We asked the following four questions:

- Which protected areas are currently important refugia for Blanding's turtle in Wisconsin?
- What is the current pattern of functional connectivity among those protected areas?
- How might climate and land use change affect the importance of those protected areas in the future under different emissions and land use scenarios?
- What is the relative effect of different combinations of economic policy and emissions scenarios on connectivity?

2. Methods

2.1. Study species

We modeled habitat connectivity for the Blanding's turtle, a semi-aquatic species with a center of distribution around the Great Lakes, ranging from Nebraska to Maine and north to Ontario and Nova Scotia (Congdon and Keinath, 2006). The species is listed as threatened or endangered in many states within its range (Mockford et al., 2006), is a 'species of concern' in the U.S. Fish and Wildlife Service Midwest Region (<https://www.fws.gov/midwest/es/soc/>), and is listed as Endangered on the IUCN Red List (Van Dijk and Rhodin, 2011). Blanding's turtle is a species of special concern in Wisconsin due to observed population declines and habitat vulnerability (Wisconsin Department of Natural Resources, 2014). While Blanding's turtle was removed from the Threatened Species List in Wisconsin in 2014, the species was designated a protected wild animal the following year (Wis. Admin. Code NR. § 10.02(11) ({2015})).

After the Wisconsin glaciation, the Blanding's turtle moved north- and eastward from several potential refugia to occupy its current range (Mockford et al., 2006; Rödder et al., 2013; Schmidt, 1938). Blanding's turtles make use of a wide variety of habitat types, ranging from wetlands and permanent water bodies used for foraging and overwintering, to upland habitats used for movement among wetlands and terrestrial nesting (Congdon and Keinath, 2006). In Wisconsin, these habitats include shallow freshwater ponds, marshes, river backwaters, ditches, and impoundments hosting areas with a mix of open water and dense submergent and emergent vegetation (Ross and Anderson, 1990).

2.2. Study area and current habitat suitability

Our study area was the state of Wisconsin. To create a habitat suitability map, we first created a model of habitat suitability for Blanding's turtle over its entire U.S. range from 229 known occurrences spanning 1993–present, available in the Global Biodiversity Information Facility (GBIF; <http://www.gbif.org/>) and 115 additional locations (unpublished data from co-authors BR, MZP; location points were restricted to one point per 1 km). We employed Maxent software (version 3.3.3) (Phillips et al., 2006), a machine learning program that uses presence-only species records to model distributions and is widely applied because it regularly outperforms other algorithms in its predictive power (Elith et al., 2006; Elith and Graham, 2009; Hijmans and Graham, 2006; Stryzowska et al., 2016). We used default Maxent settings (Phillips and Dudík, 2008) with the exception of the removal of threshold and hinge features to provide more ecologically realistic response curves and more general predictions (Bateman et al., 2012b). We created a range-wide model to ensure that we captured the full range of variability of Blanding's turtle habitat, and did so by randomly generating 10,000 pseudo-absence locations within 100 km of the 334 known occurrence locations and comparing environmental conditions between pseudo-absences and occurrences (as per VanDerWal et al., 2009). Our environmental layers included one climate layer (mean annual temperature from 1961 to 1990) and “distance to” eight land use classes based on a reclassification of the 2006 National Land Cover Dataset (Fry et al., 2011). Within the Maxent framework, each Blanding's turtle location point (and pseudo-absence point) was evaluated against nine values. One was the mean annual temperature and the other eight values were the distance to the nearest occurrence of each of the land use classes. We focused on land use classes because current land use has been shown to be dominant in structuring populations for this species (Reid and Peery, 2014). The land use classes we used were: open water (NLCD class 11), crop (class 82), pasture (class 81), forest (classes 41, 42 and 43), urban (classes 21, 22, 23 and 24), rangeland (classes 52 and 71), woody wetlands (class 90), and emergent herbaceous wetlands (class 95). We used climate data from the Research Program on Climate Change, Agriculture and Food Security (CCAFS) data portal (<http://ccafs/climate.org/>). We resampled all environmental layers to 500-m resolution to increase ease of computation for subsequent analyses of landscape resistance and because Blanding's turtles may range over areas considerably greater than this resolution over the course of their lifetime. We then mapped current suitability for the entire state of Wisconsin based on the parameters from the range-wide model.

We used the suitability output from the Wisconsin-wide projected model to identify what are, under current conditions, the 250 most important protected areas for Blanding's turtle from among all class 1 and 2 protected areas in the U.S. protected area database (<http://gapanalysis.usgs.gov/data/padus-data/>) within Wisconsin. Class 1 and class 2 protected areas provide the highest degree of protection and are typically managed for biodiversity regardless of ownership and include, for example, National Parks and Wilderness Areas. Whereas in protected areas of other classes, resource extraction or other human use is allowed. We determined rank of Wisconsin protected areas based on the total amount of habitat area with probability of Blanding's turtle suitability values in the highest 0.1 increment bin of suitability, > 0.9 (based on the Maxent logistic probability of occurrence scale, estimated between 0 and 1). We chose to select areas within this high suitability bin in order to rule out unsuitable sites and focus on the most optimal locations for this species (Pearce and Ferrier, 2000; Pearson, 2007). Also, because a focus of our work was connectivity, we did not impose a minimum size threshold on suitable habitat patches, as smaller patches can function as stepping stones, enhancing connectivity (Krosby et al., 2010).

Finally, we used the “maximum training sensitivity plus specificity” threshold in Maxent to determine cut-off for suitable vs. unsuitable

habitat. This threshold is relatively conservative (high omission rate) and for this model had a probability of occurrence value of 0.34 (based on the logistic value score 0–1), below which we deemed sites as unsuitable. Above this threshold, we divided the suitable range into two classes: moderately suitable (probability of occurrence values between 0.34 and 0.66) and highly suitable (> 0.66 probability of occurrence). We totaled the amount of unsuitable, moderately suitable, and highly suitable habitat for each of the 250 protected areas as well as for the entire state of Wisconsin. We evaluated model performance based on the area-under-the-curve (AUC) score.

2.3. Future habitat suitability

To estimate future habitat suitability we created a second habitat suitability map for Wisconsin, based on future projected land cover, using output from an econometric model (Hamilton et al., 2013; Radeloff et al., 2012) and future projected annual mean temperature based on two different climate change emissions scenarios. We used the Maxent “fade-by-clamping” option, which removes areas with the most novel conditions (i.e., values furthest outside of the training range of data) from the final model predictions but allows for some extrapolation within conditions near in value to that of the training range of data (Phillips et al., 2006). The econometric model is based on observed land-use changes between 1992 and 1997 from the National Resources Inventory, county-level net economic returns and soil productivity. It provides estimated land-use transition probabilities for crop, pasture, forest, urban, and rangeland from 2001 to 2051. The inputs to the model can be adjusted to represent different economic policies and generate alternate maps of future land-use change patterns.

We evaluated future changes in connectivity through application of two economic policy scenarios. The first scenario, the “baseline”, reflects a continuation of the land-use change patterns seen between 1992 and 1997. The second scenario, “pro-agriculture”, reflect an increase in the net economic return for agricultural land-use of 10% every 10 years. We chose these scenarios because in previous analyses they exhibited notable differences in terms of future conditions, and because the increasing economic returns in the pro-agriculture scenario reflects recent economic conditions (Hamilton et al., 2015). Landscape genetic analyses have also identified agriculture as a barrier to gene flow in Blanding's turtle (Reid et al., 2017). Therefore, differences in the degree of projected agricultural intensification are highly relevant to current and future connectivity. The land use classes in the scenarios were identical to those we used in the “current suitability” map. Since pixel-specific changes are difficult to predict, we generated 10 replicates of each of the economic policy scenarios (see below).

For our future climate data, we used “low” and “high” emissions-based climate change scenarios. We analyzed 2050s output from the MIROC 3.2 hi-res General Circulation Model (GCM) under the SRES A1B scenario model for our high emissions climate change scenario, and the MRI CGCM 2.3.2a GCM under the SRES B1 model for our low emissions climate change scenario. To maximize contrast in potential future conditions we selected the models with the strongest and weakest effects on climate change that covered our study region at 30-second resolution.

Finally, we modeled future habitat suitability for each possible combination of our climate and land use scenarios to generate habitat suitability maps for Blanding's turtle. This resulted in 40 future habitat suitability maps (2 economic policy scenarios × 10 replicates of each economic policy scenario × 2 emissions scenarios). We summed the amount of unsuitable, moderately suitable, and highly suitable habitat within the 250 protected areas as well as for the entire state of Wisconsin using the mean values of the 10 economic policy scenario replicate/emission scenario ensembles for each of the 4 economic policy/emissions scenario combinations.

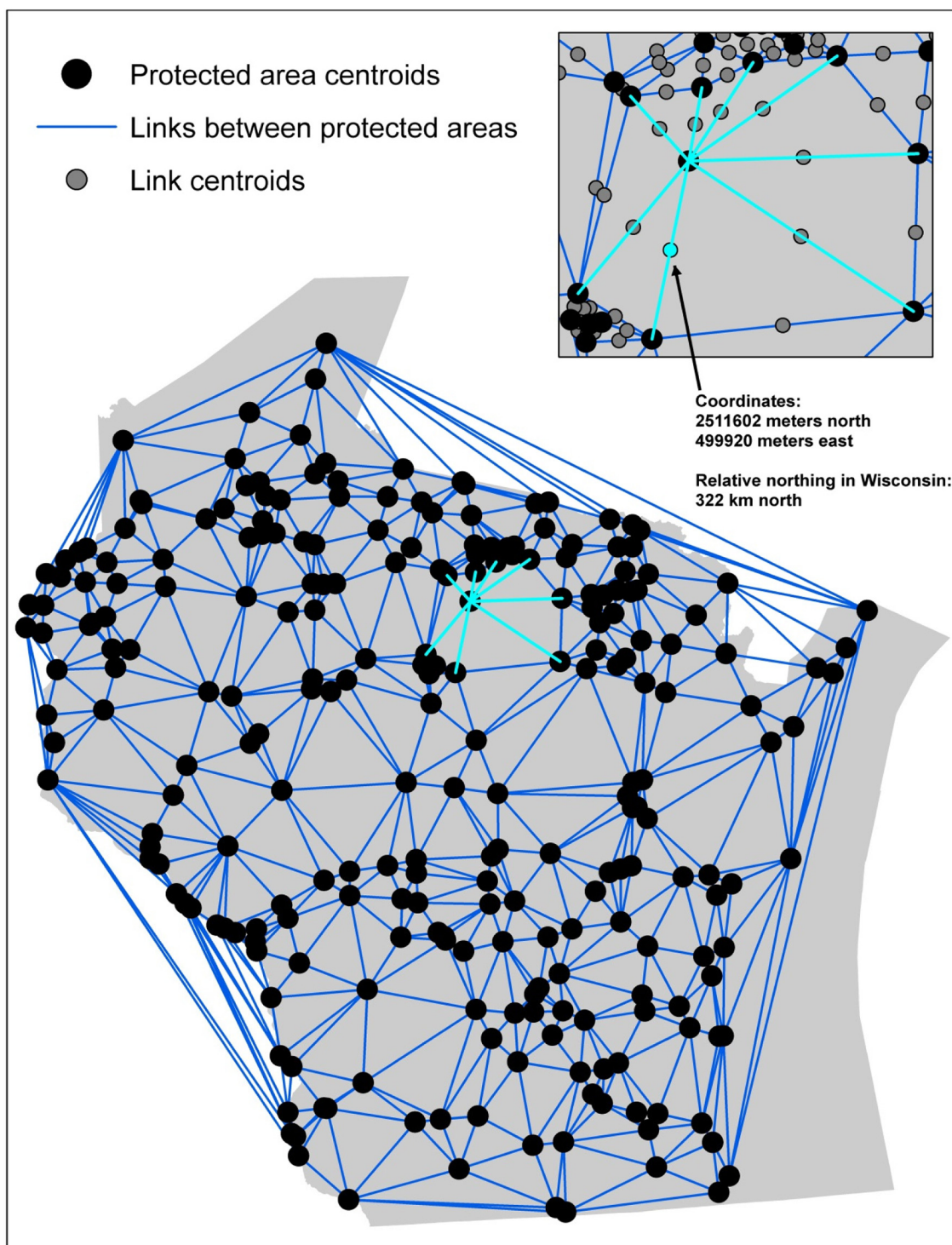


Fig. 1. Triangulated irregular network representing priority protected areas for Blanding's turtle in Wisconsin. The inset shows the connections to relevant neighbors for one protected area. The centroid for one link is highlighted and the geographic coordinates and relative northing within Wisconsin for that centroid are provided.

2.4. Connectivity

We quantified connectivity among protected areas using a triangulated irregular network (TIN), a standard GIS data structure that can be used to identify nearest relevant neighbors, and used a subset of those connections for comparison among the scenario combinations (Longley et al., 2005; Fig. 1). Due to computational processing limitations, we used a random sample subset of the data for analyses, thus we evaluated only 195 connections rather than the > 62,000 possible connections.

To determine the functional distances for each of the 195 connections we used Circuitscape (McRae and Shah, 2009), a software package employing circuit theory to quantify landscape connectivity. Circuitscape is distinctive among habitat connectivity measurement tools in that it allows for the possibility of more than one path connecting two habitat patches. This is more realistic from an ecological perspective than a least-cost path approach, in which connections between patches are restricted to a single path, when there may in fact be many paths connecting two habitat patches (McRae et al., 2008). The

distances generated in Circuitscape are “resistance distances” based on the difficulty of traversing the landscape. Resistance distances do not equate to geographic distance, but they do scale linearly (McRae et al., 2008), meaning that estimated distances are relative (e.g., a resistance distance of 2 is twice as “far” as a resistance distance of 1) and that the relative difficulty of traversing a network of habitat patches can be compared among networks and over time. We used the habitat suitability maps generated from Maxent as “conductance” (i.e., ease of movement) inputs in Circuitscape, with higher suitability equating to higher conductance. The output from Circuitscape was a table of resistance distances between patches within our protected area network.

As with the habitat suitability maps, we generated mean change in resistance distance among the 10 replicates of each of the 4 economic policy-emission scenario combinations.

We tested whether changes in the resistance distances were larger among policy or emissions scenarios and whether the changes varied by geographic location. We accomplished this by first identifying the mid-point of the 195 connections from the TIN and including the relative “northing” (with 0 being the southernmost location) of each of those points as a value in subsequent analyses (Fig. 1). We regressed mean proportional change in resistance distance for the connections against their northing, resulting in 4 curves, each of which represented the

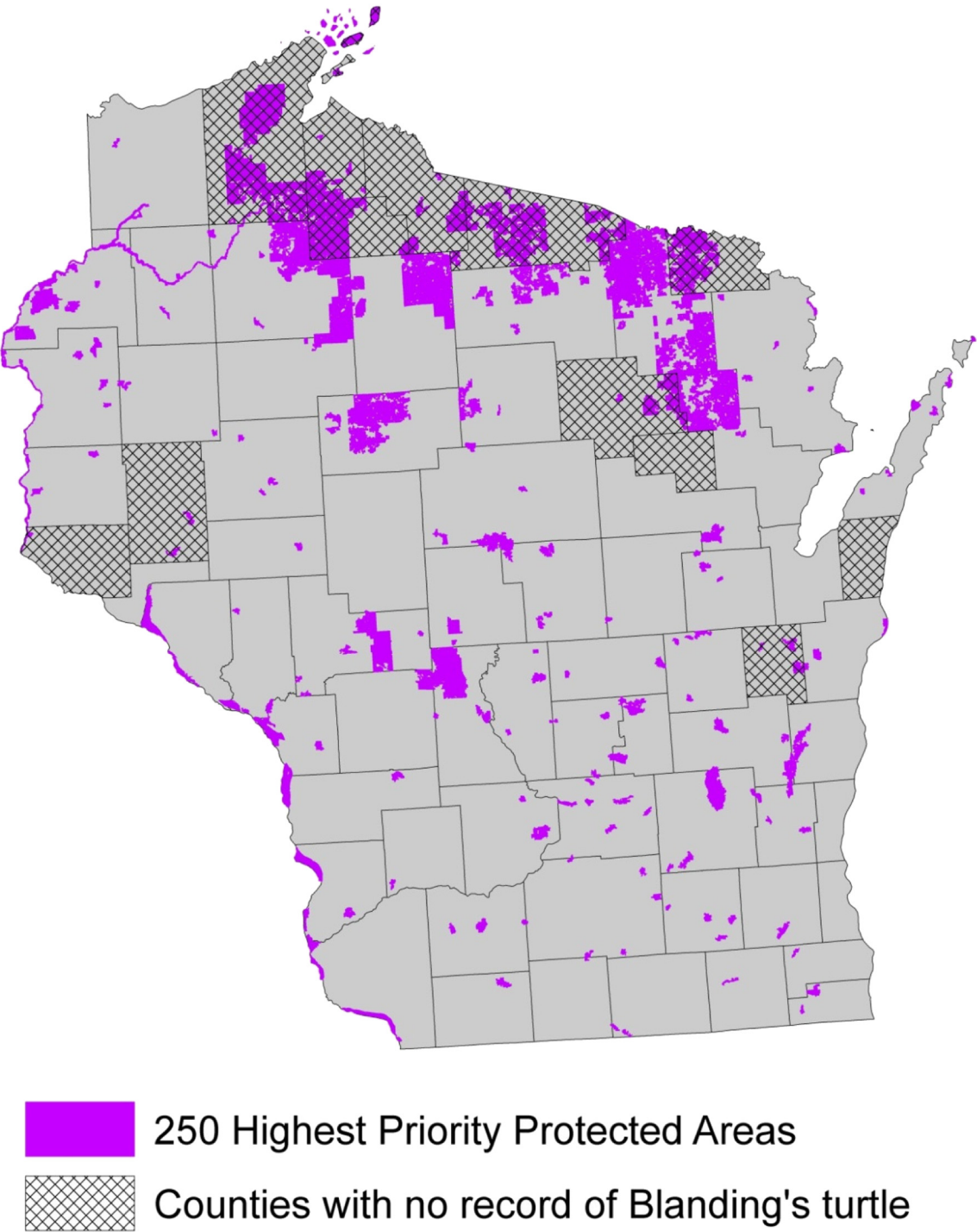


Fig. 2. Map showing the distribution of the 250 highest-priority current protected areas for the Blanding's turtle and those counties with no recorded occurrence of the species.

effect of geography under a different scenario.

3. Results

3.1. Current habitat suitability in Wisconsin

The range-wide model had an AUC score of > 0.92 , thus discriminating highly suitable habitat well (Fig. A1), and from the parameters in this model, we constructed a Wisconsin model of habitat suitability. The highest priority protected areas (based on the 0.9 probability of suitability criterion) were distributed across the state, with the majority found in northern Wisconsin (Fig. 2). More than 10% (31 of the 250) of protected areas containing the most habitat with probability of suitability values > 0.9 (i.e., highest priority refugia) for Blanding's turtle were located within counties with no history of Blanding's turtle occurrence as of 2017 (Fig. 2). Emergent herbaceous wetland (land use class 95), urban land (class 4), open water (class 0), and mean annual temperature were the most important variables predicting Blanding's turtle suitability (AUC = 0.898) with 29, 17, 15, and 13% relative contribution, respectively. Most of Wisconsin (14.2 million ha) is currently unsuitable for the Blanding's turtle, but there are approximately 2.4 million ha of moderately suitable habitat (probability of suitability between 0.34 and 0.66), and 0.3 million ha of highly suitable habitat (> 0.66) (Figs. 3, 4).

The 250 priority protected areas for Blanding's turtle included 70,000 ha of highly suitable habitat under current conditions (Fig. 5). The amount of highly suitable habitat within priority protected areas ranged from 0 to 11,600 ha (\bar{x} = 269 ha), with 0 to 24,800 ha

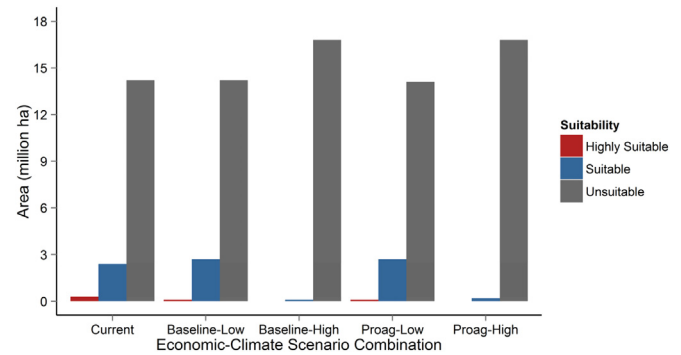


Fig. 4. Areal distribution of habitat suitability for highly suitable, suitable, and unsuitable habitat within the entire state of Wisconsin.

(\bar{x} = 1021 ha) of moderately suitable habitat, and 0 to 126,900 (\bar{x} = 3200 ha) of unsuitable habitat. The proportion of land area within protected areas providing highly suitable habitat (0.06) and moderately suitable habitat (0.23) were both greater than these proportions within the state of Wisconsin as a whole (0.02 and 0.14, respectively).

3.2. Future habitat suitability

Changes in habitat suitability were largely driven by changing climate. Suitable habitat for the turtle shifted northward under both the low and high emissions scenarios, with relatively widespread suitability in the southern 2/3 of the state under the low emissions scenario and

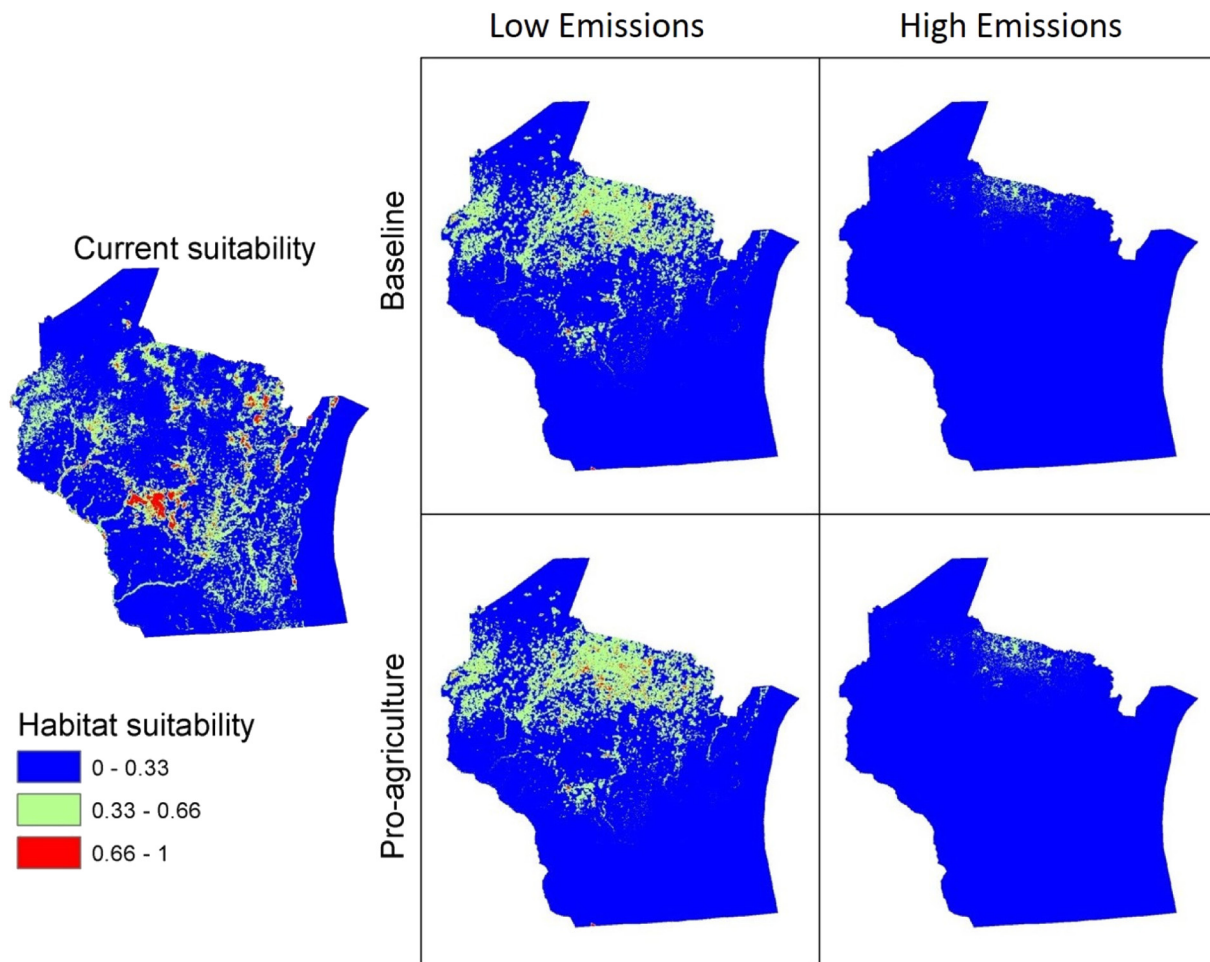


Fig. 3. Habitat suitability maps for Blanding's turtle under current conditions and 4 combinations of future land-use and climate scenarios projected for the 2050's.

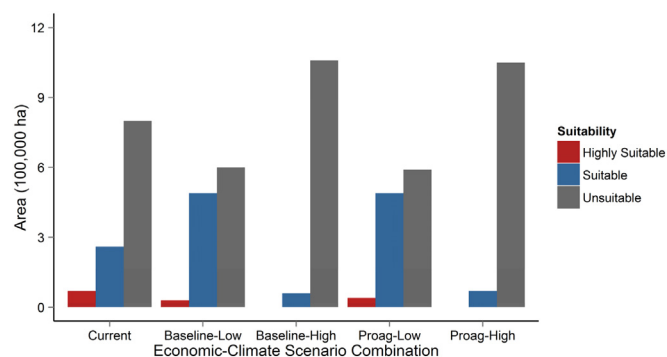


Fig. 5. Areal distribution of habitat suitability for highly suitable, suitable, and unsuitable habitat within the 250 most important protected areas for Blanding's turtle in Wisconsin.

with suitable habitat remaining only in northern Wisconsin under the high emissions scenario (Figs. 2, 3). The shift in habitat suitability was such that 158 and 160 of the original 250 priority protected areas for Blanding's turtle retained any suitable habitat under the low-emissions/baseline and low-emissions/pro-agriculture scenario combinations, respectively. The changes were even stronger under the high-emissions/baseline and high-emissions/pro-agriculture scenarios with only 35 and 39 protected areas retaining any suitable habitat, respectively.

Across Wisconsin, under the low-emissions scenario, both economic-policy scenarios resulted in nearly identical and minor increases in available habitat, with small increases in moderately suitable habitat offsetting smaller decreases in highly suitable habitat (Figs. 3, 4). Within priority protected areas, under the low-emissions scenario, the pro-agriculture economic policy scenario resulted in slightly more moderately suitable habitat than the baseline scenario (494,150 ha and 488,500 ha, respectively) and slightly more highly suitable habitat as well (39,000 ha and 30,025 ha, respectively; Tables 1, 2). Within priority protected areas the proportion of moderately suitable habitat under the baseline and pro-agriculture economic policy scenarios (0.44 in both cases) and the proportion of highly suitable habitat (0.03 in both cases) was higher than the proportion of moderately suitable habitat and highly suitable habitat in Wisconsin as a whole (0.16 and 0.006, respectively).

Under the high emissions scenario there was a complete loss of highly suitable habitat and large decreases in moderately suitable habitat, regardless of economic policy scenario, and moderately suitable habitat was restricted to a small region within northern Wisconsin (Figs. 3, 4). The pro-agriculture policy scenario again resulted in more moderately suitable habitat (72,475 ha) than the baseline economic scenario (60,925 ha; Table 1). However, under the high emissions scenario there was no highly suitable habitat within all of Wisconsin regardless of the economic scenario (Figs. 3, 5, Table 2). In addition, the areas with suitable habitat were largely located in Wisconsin counties where Blanding's turtle is not known to occur currently (Figs. 2, 3).

Table 1

Amount of moderately suitable habitat for Blanding's turtle in priority protected areas under the combinations of high/low emissions climate and baseline/pro-agriculture (Proag) economic policy scenario.

Area (ha)	Moderately suitable			
	Low emissions		High emissions	
	Baseline	Proag	Baseline	Proag
Upper range	48,150	50,150	22,425	24,875
Lower range	0	0	0	0
Total	488,500	494,150	60,925	72,475
Mean	1954	1976	243.7	289.9

Table 2

Amount of highly suitable habitat for Blanding's turtle in priority protected areas under the combinations of high/low emissions and baseline/pro-agriculture (Proag) economic policy scenario.

Area (ha)	Highly suitable			
	Low emissions		High emissions	
	Baseline	Proag	Baseline	Proag
Upper range	6000	7100	0	0
Lower range	0	0	0	0
Total	30,025	39,000	0	0
Mean	120.1	156	0	0

Under the high-emissions scenario priority protected areas retained suitable habitat in higher proportions under the baseline (0.05) and pro-agriculture scenarios (0.06) than the remainder of Wisconsin (0.006 and 0.01, respectively).

3.3. Connectivity resistance distances

Relative changes in resistance distance between protected area pairs increased more quickly in southern Wisconsin than in northern Wisconsin under all future scenarios (~100,000-fold increase and ~34-fold increase, for high and low emissions scenarios respectively, in resistance to landscape movement in the south compared to the north), reflecting large decreases in connectivity and concurrently, large increases in resistance among protected areas, especially in the south. The differences in connectivity among the scenario combinations were largely due to climate change, (Fig. 6). For a given emissions scenario,

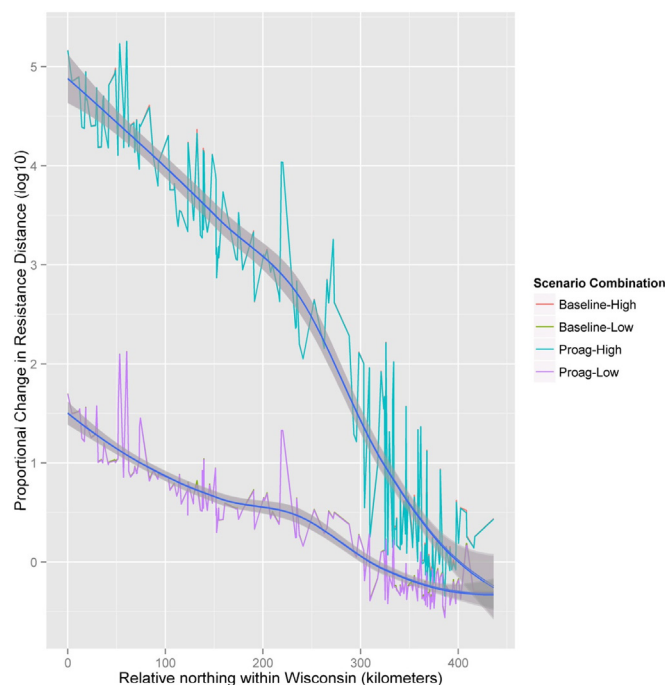


Fig. 6. Comparison of the proportional change (log base 10) in resistance distance among scenario combinations. The x-axis represents the northings of the centroids of connections between protected areas ranging from south to north in Wisconsin. The values on the y-axis reflect the proportional change in resistance distances between the protected area pairs. Y axis values are the power to which 10 is raised (i.e.; $3 = 10^3$, i.e. a 1000-fold increase in landscape resistance to movement) for the proportional changes in resistance distance. Given the log scale, the rate of change in resistance distance is exponentially higher for the more southerly connections. Both baseline scenario combinations are overlapped by the Pro-agricultural scenario.

differences among economic policy scenarios were close to zero in all cases, and they were highly correlated ($r > 0.99$), making the economic policy scenarios indistinguishable from one another from the perspective of landscape connectivity for Blanding's turtles (Fig. 6). In contrast, in northern Wisconsin, habitat connectivity improved relative to current conditions under the low emissions climate scenario, and this was also the case for the high emissions climate scenario, but improvements were smaller (Figs. 6, 3). Changes in landscape resistance to turtle movements were essentially zero at approximately 300 km north (low-emissions climate scenarios) and 400 km north (high-emissions climate scenario) of the southern Wisconsin border, with differences between the emissions scenarios nearly zero at the northern limits of Wisconsin (Fig. 6). The centers of zero change in resistance distance essentially track the changes in habitat suitability (Figs. 6, 3). Finally, while protected area connectivity improved in northern Wisconsin, the absolute value of improvements was minor compared to the substantial decrease in connectivity in southern Wisconsin (Fig. 6).

4. Discussion

We predicted substantial future changes in habitat suitability and connectivity of Wisconsin's protected areas for Blanding's turtle by the 2050s. The changes in protected area importance, habitat suitability, and protected area connectivity were largely driven by climate change, as indicated by the notable differences between the high- and low-emissions scenarios that we evaluated. The two economic policy scenarios that we evaluated were nearly identical in their effects on protected areas and habitat connectivity, probably because the effects of climate change were so much greater and essentially swamped effects of differences in land use. Under all scenarios, our habitat models predicted significant northward shifts in habitat suitability and, therefore, protected area of importance for Blanding's turtle. In addition, changes in habitat suitability were predicted to occur at a higher rate in southern Wisconsin, where landscape resistance to movement among protected areas was projected to become orders of magnitude greater. It is worth noting that habitat suitability values in southern Wisconsin are already relatively low, possibly indicating that existing populations could be “legacy” populations that mainly persist because of Blanding's turtle longevity. Our findings expand on other research showing a poleward shift in habitat suitability as well as substantial changes in protected area suitability and connectivity for many species (Parmesan and Yohe, 2003; Piquer-Rodríguez et al., 2012; Thuiller, 2004) and are unique in the relative changes in landscape resistance they demonstrate.

Our results indicate that there are substantial areas of apparently suitable habitat in portions of Wisconsin where Blanding's turtle is not currently found. This is not entirely surprising. Blanding's turtle's range contracted southward and westward during the Pleistocene and expanded northward since the retreat of the glaciers (Schmidt, 1938; Stephens and Wiens, 2009). Dispersal back northward is a slow and ongoing process, made much more challenging by extensive human transportation networks that pose barriers to movement and species survival (Beaudry et al., 2008; Bennett et al., 2011; Cushman et al., 2013; Gerlach and Musolf, 2000; Keller and Largiadèr, 2003; Shepard et al., 2008). Although Blanding's turtles will occasionally use patches of unsuitable habitat for small scale movement, as the amount of unsuitable habitat increases, survival of dispersing individuals will undoubtedly decline. As climate changes, northward movement will have to accelerate if Blanding's turtles are to keep pace with the climate space they currently occupy, but there are several fortunate artifacts of the Wisconsin protected area network that may facilitate Blanding's turtle to adapt to changing conditions. Blanding's turtles use complexes composed of multiple wetlands (Beaudry et al., 2009) and our results reflect a strong association of the species with emergent wetland habitat embedded in forests. The largest protected areas in Wisconsin are found in northern Wisconsin where most of the unoccupied areas currently

occur. This may be good news for Blanding's turtle if they can successfully disperse northward, given that their suitable habitat is predicted to shift northward. In addition to their large size, those protected areas are also likely to harbor disproportionate amounts of wetland habitat since wetlands are well represented within Wisconsin's protected area network (Carter et al., 2014). It is an open question whether Blanding's turtle populations can successfully disperse to available habitat, as natal dispersal appears to be low while breeding dispersal appears to be relatively high (Reid et al., 2016). Adult turtles exhibit long-term fidelity to aquatic habitats (Congdon et al., 2011) and terrestrial nesting habitats (Reid et al., 2016), potentially limiting the capacity for shifts in range. However, extensive gene flow among nearby wetlands (McGuire et al., 2013) and occasional breeding and natal dispersal (Reid et al., 2016) as well as individual movements of > 17 km within a single active season (Beaudry et al., 2010) indicate some potential for responding to shifts in climate via rare long-distance dispersal events.

The strong northward shift in habitat suitability even under the low-climate change scenario is startling but not unprecedented. Shifts in habitat suitability from climate change is already outpacing the capability of many species to adapt in situ or to disperse to areas with suitable environmental conditions (Loarie et al., 2009; Thuiller, 2004; Veloz et al., 2011; Williams and Jackson, 2007). The changes in distribution suggested by our model, and the consequences to Blanding's turtle, are similar to eastern Massasauga rattlesnake (*Sistrurus catenatus catenatus*) range changes, which are also largely due to climate change (Pomara et al., 2013). Biogeography and habitat preferences of Blanding's turtle and eastern Massasauga rattlesnake are similar and both followed a similar historical change in distribution following the Pleistocene glacial retreat (Schmidt, 1938). The nearly complete loss of suitable habitat for Blanding's turtle from Wisconsin in the foreseeable future is particularly sobering given that current magnitude of change anticipated. Effects of future climate change on habitat suitability may have serious consequences for Blanding's turtle habitat corridors and stepping stones. Our models suggest that suitable habitat will be outside the range currently experienced by the Blanding's turtle in the southern 1/3 (under low-emissions scenario) or the southern 3/4 (under high-emissions scenario) of Wisconsin what likely is increasing resistance of the landscape to natural dispersal through the use of habitat corridors as time progresses. Furthermore, the effects of climate on habitat suitability were projected to be so strong that even developing stepping stone corridors for facilitating movement to new habitat would be ineffective at supporting turtle dispersal (Baum et al., 2014; Kramer-Schadt et al., 2011; Saura et al., 2013). Even under the low-emissions scenario, habitat suitability is decreasing faster than the turtle is likely able to disperse. Our results clearly demonstrate an alarming “trailing edge” effect, where species respond more slowly at the trailing edge of a shifting climate space (Anderson et al., 2009). Previous studies have indicated that the leading and trailing edges of suitable habitat (based on climate conditions) move at different speeds because they are driven by slightly different mechanisms (Anderson et al., 2009; Loarie et al., 2009). Whereas the extent of our analysis did not allow us to model change at the leading edge of the Blanding's turtle's suitable habitat, our results indicate different rates of change across the projected distribution of Blanding's turtle, with the decrease in habitat suitability at the trailing edge occurring at an exponentially faster rate than in the core of the projected distribution. This compounds an already bleak outlook for a species with limited dispersal capability, such as Blanding's turtle.

While we emphasize the strong impact of climate in our models of future distribution of suitable habitat, we do not mean to imply that land use change is not an important factor. We interpret the lower importance of land use in our models as an indication that land use conditions as they currently stand are already problematic. Indeed, the fact that Blanding's turtle is of conservation concern is directly attributable to land use and habitat fragmentation (Attum et al., 2008; Beaudry et al., 2008). It is possible that habitat suitability of Blanding's

turtle might be limited at the south edge of its range by competition from other turtle species (e.g., red-eared slider, *Trachemys scripta*), as is the case for other species of conservation concern (e.g. Bateman et al., 2012a). However, a more likely explanation is that that Blanding's turtle distribution is linked to climate, which is the case for the distributions of other members of the Emydidae family, which also have a northern orientation (Stephens and Wiens, 2009). Blanding's turtle distribution has been shown to be strongly limited by climate (Rödger et al., 2013). The projected temperature increases within the timeframe of our study are not likely to exceed the physiological tolerance of adult turtles but they may be significant enough to exceed the range of temperatures under which egg incubation is successfully (Mockford et al., 2006). The relative effects of climate versus land use on habitat suitability and future landscape connectivity may be very different for a species whose distribution is limited by habitat availability more than by climate.

There are limitations of our analyses. First, there is significant temporal variation in wetland area both seasonally and inter-annually, and this affects habitat suitability for Blanding's turtle given that the turtles typically use a mosaic of wetlands throughout their active season (Beaudry et al., 2009; Niemuth et al., 2010). In fact, our approach disregards the seasonally and inter-annually dynamic nature of wetlands and the impacts of extreme drought on wildlife species (Albright et al., 2009; Niemuth et al., 2010). Given that wetlands were the most important predictor of Blanding's turtle occurrence in our models, alterations of wetland temporal and spatial extent would further alter habitat suitability and protected area connectivity for Blanding's turtle. The land use change model we used does not predict changes to wetlands because the econometric models of land use change reflect that wetland area has largely remained constant in recent decades (Dahl, 2011; Nusser and Goebel, 1997). Thus, we treated wetlands as a static element in the environment, keeping their area and extent constant over the 50-year timeframe of our analysis because it is unlikely that wetlands will change in their land use even though changes in hydrology and their subsequent suitability to Blanding's turtles may occur.

While our model highlighted urban lands as being important for Blanding's turtle, we suspect may reflect some observation bias since turtles near roads are more likely to be reported than turtles far from roads (Kadmon et al., 2004). In addition, although turtles can be attracted to urban areas such as roads and residential lawns because they provide attractive nesting sites, these areas are also ecological sinks that actually are associated with increased turtle mortality (Beaudry et al., 2008; Grgurovic and Sievert, 2005; Steen et al., 2006). Future research efforts could combine movement data of telemetered animals and population genetic structure to better understand habitat sources and sinks.

Our study reaffirmed what has been demonstrated in prior research, in that future land use and climate changes will only exacerbate what are already challenging landscapes for many native species (Hamilton et al., 2015; Pomara et al., 2013). The strategy of restoring habitat corridors, while intuitively appealing and relatively feasible given the tools available to land managers, may be limited given that land use change has already isolated many protected areas. Substantial investments would be necessary to significantly improve connectivity even under static climatic conditions (Hamilton et al., 2015). Our results indicate that the velocity of climate change is too high to mitigate climate change effects solely by improving habitat connectivity, especially for less mobile species for which rates of change outpace their ability to keep up.

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